Insecticide Susceptibility in *Coptotermes formosanus* and *Reticulitermes virginicus* (Isoptera: Rhinotermitidae)

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ABSTRACT Lethal time to mortality responses were established for eight insecticides against workers and soldiers of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, and workers of *Reticulitermes virginicus* (Banks). There were significant differences in the tolerance ratios between workers of *C. formosanus* colonies to all toxicants tested except fipronil. One colony was 16 times more tolerant than another to deltamethrin. *C. formosanus* soldiers had significant differences in tolerance ratios among colonies exposed to all toxicants except chlorpyrifos. Methoxychlor, permethrin, deltamethrin, and fipronil did not kill soldiers from two, one, one, and three colonies, respectively, within 8 h. Seventy-five percent of *R. virginicus* colonies were significantly less susceptible than the most susceptible colony to chlordane, methoxychlor, chlorpyrifos, cypermethrin, and fipronil, with 50% of the colonies less susceptible to permethrin and bendiocarb. In 50% of *C. formosanus* colonies the worker lethal time curves displayed substantial flattening in response to permethrin, and deltamethrin. Lethal time curves for *C. formosanus* soldiers exposed to chlordane, chlorpyrifos, permethrin, cypermethrin, deltamethrin, and bendiocarb showed substantial flattening. *R. virginicus* workers demonstrated substantial curve flattening when exposed to chlordane, methoxychlor, chlorpyrifos, deltamethrin, and fipronil. These findings indicate substantial inter-colony and intra-colony differences in susceptibility to insecticides.

KEY WORDS *Coptotermes formosanus*, *Reticulitermes virginicus*, termite, insecticide susceptibility, resistance

SUBTERRANEAN TERMITES CAUSE considerable damage to homes and other structures. Over one billion dollars are spent annually on termite prevention, control, and repair measures in the United States (Potter 1997). Termite control appears to be more difficult in the postchlordane era even with the newest chemicals and technologies (Gold et al. 1996, Potter 2000).

Despite the economic impact of subterranean termites, little is know about the differential effects of insecticide intoxication on colonies. Effectiveness of termiticide treated soil against subterranean termites depends not only upon the nature and quantity of the toxicant and the soil properties but also on the response of the termites to the insecticide. Treatment failures may be due to differences in toxicity, repellency, speed of intoxication, and vapor pressure characteristics of termiticides (Su et al. 1982). The possibility that differences in termite susceptibility to insecticides exist should be taken into consideration.

This article reports the results of a laboratory study designed to determine inter-colony differences in susceptibility of the Formosan subterranean termite, *Coptotermes formosanus* Shiraki, and *Reticulitermes virginicus* (Banks), to eight toxicants including chlordane, methoxychlor, chlorpyrifos, bendiocarb, permethrin, cypermethrin, deltamethrin, and fipronil.

Materials and Methods

Four colonies each of *C. formosanus* and *R. virginicus* were obtained from field sites in New Orleans, LA, and north Florida, respectively. *Coptotermes formosanus* colonies S9, S7, and S19 were collected from the Southern Regional Research Center, United States Department of Agriculture, and colony U8 was collected from the University of New Orleans, New Orleans, LA; *Coptotermes formosanus* were collected from bucket traps (Su and Scheffrahn 1986) and maintained on stacked, moistened spruce (*Picea* sp.) slats (10 by 4 by 0.5 cm) in plastic containers (13 by 13 by 4 cm) at ≈100% RH and 26°C. *Reticuliteres virginicus* colony C2 was collected from a wooden porch at Jacksonville Naval Air Station, Jacksonville, FL. Colonies C21 and C26 were collected from pine (*Pinus* sp.) logs within a roadside stand of pine trees at the Alachua County fair grounds, Gainesville, FL. Colony C71 was collected from a pine log within a stand of pine trees at the University of Florida's natural area teaching laboratory, Gainesville, FL. Wood infested with *R. virginicus* was maintained in plastic trashcans (43 cm diameter by 65 cm high) with moist vermiculite at its bottom at ≈23°C. *Retiulitermes virginicus*

was extracted from the maintained infested wood with rolled moistened corrugated cardboard (10 cm diameter by 15 cm high) as per La Fage et al. (1983). Termites were identified using soldier keys from Miller (1949), Scheffrahn and Su (1994), Su et al. (1997) and Banks (1920). All termites were tested within 30 d of their collection.

Termites were tested for their susceptibility to insecticides by exposing them to a filter paper surface treated with known amount of toxicant (Su et al. 1987). Whatman filter paper (No. 1, 10 mm diameter, Whatman, Hillsboro, OR), was placed on the flat bottom of a glass vial (11 mm i.d. by 45 mm high). A toxicant dissolved in 50.0 μl of spectrophotometric grade acetone was pipetted onto the filter paper and the acetone was allowed to evaporate. Insecticide was therefore deposited on the filter paper on the bottom of the vial. Filter paper was used as the substrate instead of depositing the toxicant directly on the glass because some pyrethroids left a sticky residue on the glass surface that interfered with evaluation of termite mortality. A diagnostic concentration of insecticide was established empirically in preliminary studies. The doses were selected on the basis of achieving a reasonable lethal time to mortality (LT) value of ≈60 min for the most sensitive strains. Toxicants used in this study were technical grade, except for chlordane, and obtained from Chem Service (West Chester, PA). The name, purity, and dose tested were as follows. Acetone (control), 50.0 μl, spectrophotometric grade, chlordane, 45% Chlordane Concentrate Termite Control with 50% petroleum distillate and 5% inert ingredients formerly manufactured by Federal Chemical Company (Indianapolis, IN) (630.65 μg/cm^2); methoxychlor (a DDT analog), 100% (5.261 mg/cm^2); chlorpyrifos 99.0% (526.13 μg/cm^2); permethrin, 99.5% (5.261 μg/cm^2); cypermethrin, 88% (5.261 μg/cm^2); deltamethrin, 99.2% (0.053 μg/cm^2); bendiocarb, 76.0% (2.63 μg/cm^2); fipronil, 96% (630.65 μg/cm^2); and fipronil, 96% (630.65 μg/cm^2) + oil (526.13 μg/cm^2). Oil was Three-In-One Household Oil manufactured by Boyle-Midway (New York, NY).

Ten workers of at least third instar, as determined by size, or soldiers were placed in four similarly prepared vials (replicates). *Coptotermes formosanus* worker masses were determined by weighing four groups of 10 termites from each colony. Mortality was recorded at intervals of 5 min and at 20-min intervals if the tests progressed beyond 100 min. Data were recorded until at least 90% of the insects were dead or up to 8 h. Data from the four replicates were pooled and analyzed by probit analysis (Finney 1971). Lethal time to 50% mortality (LT$_{50}$s) and 90% mortality (LT$_{90}$s) were estimated for each colony tested against each insecticide. The test for statistical significance between appropriate LT values was failure of their 95% fiducial limits to overlap. Comparison of the slopes was made using a likelihood ratio test of parallelism where the slopes of the probit lines are constrained to the same line. The hypothesis that the lines are parallel cannot be rejected when $P > 0.05$ (Robertson and Preisler 1992).

Tolerance ratios of two estimated LT$_{90}$ doses and their 95% CL for i = 1,2 were calculated based on estimates for the intercepts (α) and slopes (B) of two probit lines and estimates of their variance-covariance matrixes as follows: ratio = 10^a; lower limit = $10^{a\ -2\ \sigma}$; upper limit = $10^{a+2\sigma}$; with $\theta_i = (1.28-\alpha_i)/B_i$; and var $(\theta_i) = (1/B_i^2)[\text{var}(\alpha_i) + 2\theta_i \text{ cov}(\alpha_i, B_i) + \theta_i^2 \text{ var}(B_i)]$; with a = $\theta_1 - \theta_2$ and $\sigma = [\text{var}(\theta_1) + \text{var}(\theta_2)]^{1/2}$ (Robertson and Preisler 1992). This tolerance ratio estimation procedure adjusts for lack of parallelism of LT lines. A susceptibility ratio was considered significant if the 95% CL excluded one.

Results and Discussion

Mean body weight of *C. formosanus* workers (±SD, mg) are as follows: S7 = 2.52 ± 0.1; S19 = 2.33 ± 0.1, S9 = 3.70 ± 0.1, U8 = 3.02 ± 0.0. Weights of *R. virginicus* were not recorded.

Coptotermes formosanus. LT$_{50}$s, LT$_{90}$s, slopes, and tolerance ratio for *C. formosanus* are reported in Tables 1 and 2. There was no mortality in the solvent controls. Chlordane was most toxic to *C. formosanus* workers of colony S9 (Table 1; Fig. 1). Workers from colonies S7 and U8 were 6.3 and 4.9 times less susceptible, respectively, than colony S9. S9 infested two oak trees (*Quercus* sp.) along the street in front of the SRRC ≈65 m from any homes or buildings and was the most susceptible colony to chlordane. S7, S19, and U8 were all located <6 m from buildings. Theoretically, S9 could have had less contact which chlordane termiticide treatments under buildings. The small size and limited foraging range of S19 (collected from a singe bucket trap at the base of a pine tree) are indications of a young colony (Grace et al. 1995). S19 workers had a significantly steeper LT mortality slope than the other colonies, indicating a more homogenous population (Matsumura 1985). Workers from S7 had several individuals that did not die after 8 h, as indicated by the tailing dose mortality plot (Fig. 1). Soldiers from colony U8 had a tolerance ratio 20.4 times that of the most susceptible workers from colony S9. Comparison of the dose–response curve of soldiers from U8 and the other three colonies shows U8 responded differently (Fig. 1). The colony with the least susceptible soldiers, however, was only twice as tolerant as the colony with the most susceptible soldiers (Table 2). Dose–response slopes for soldiers were significantly steeper than the slopes for workers from U8, S9, and S7 but not S19. Flatter slopes indicate workers from the proposed older and larger colonies were more heterogeneous than the proposed younger, smaller S19. This may be a function of gross population numbers, an indication of differences between older versus younger workers, or multiple reproductives may have been present in the older colonies. Pooled *C. formosanus* soldiers were significantly less susceptible than workers to chlordane. Chlordane treated soldier had significantly higher tolerance ratios then the workers from their respective colonies.

Methoxychlor did not kill (0% mortality) *C. formosanus* soldiers from two of the colonies (S7 and S19)

Table 1. Insecticide susceptibility in *Coptotermes formosanus* colonies

Insecticide ($\mu g/cm^2$) stage	Colony	N	Slope ± SE[a]	LT$_{50}$ (95% FL) (min)	LT$_{90}$ (95% FL) (min)	χ^2	Susceptibility ratio LT$_{90}$ (95% CI)
Chlordane (630.65)							
Soldier	FS-S9	40	18.0 ± 2.8A	115.7 (110.1–121.9)	136.3 (127.4–162.3)	2.3	10.1 (8.9–11.5)
	FS-U8	40	19.1 ± 2.1A	236.2 (231.4–240.6)	275.8 (267.8–287.7)	2.2	20.4 (18.5–22.5)
	FS-S7	30	20.2 ± 2.3A	131.3 (128.1–134.0)	151.9 (148.1–157.5)	4.5	11.2 (10.0–12.6)
	FS-S19	30	20.2 ± 2.3A	131.3 (130.0–134.4)	154.9 (149.9–162.2)	4.5	11.4 (10.2–12.8)
Worker	FW-S9	40	11.3 ± 1.8B	10.2 (7.4–12.8)	16.5 (13.1–29.2)	2.1	1.0
	FW-U8	40	12.0 ± 1.7B	52.7 (49.2–57.9)	67.4 (60.3–91.4)	3.6	4.9 (4.3–5.8)
	FW-S7	40	8.9 ± 0.7B	61.1 (58.7–63.4)	85.2 (81.2–90.6)	6.2	6.3 (5.6–7.1)
	FW-S19	40	21.8 ± 2.7A	44.1 (37.9–47.9)	50.5 (46.7–66.5)	16.5[b]	3.7 (3.3–4.2)
Methoxychlor (5260.0)							
Soldier	FS-S9	40	13.9 ± 2.1A	97.1 (92.4–100.6)	120.1 (114.9–128.8)	0.6	0.6 (0.6–0.7)
	FS-U8	40	6.4 ± 0.6B	137.4 (128.2–145.7)	218.3 (200.1–248.5)	15.4[b]	1.2 (1.0–1.3)
Worker	FW-S9	40	6.5 ± 1.1B	211.1 (197.6–229.1)	333.0 (283.5–458.7)	0.9	1.2 (1.0–1.4)
	FW-U8	40	8.5 ± 8.5B	180.0 (172.6–186.5)	254.4 (244.0–268.2)	2.3	1.4 (1.3–1.4)
	FW-S7	40	12.1 ± 0.8A	223.3 (219.5–227.2)	284.7 (275.6–296.6)	6.2	1.5 (1.4–1.6)
	FW-S19	40	14.4 ± 1.0A	153.8 (151.0–156.5)	188.9 (183.8–195.3)	3.2	1.0
Chlorpyrifos (526.13)							
Soldier	FS-S9	40	13.3 ± 1.4A	31.6 (28.1–34.6)	39.5 (35.8–48.5)	10.5[b]	2.4 (0.5–10.6)
	FS-U8	40	11.5 ± 1.9A	32.6 (30.5–34.1)	42.1 (39.7–56.5)	0.1	2.5 (2.2–2.9)
	FS-S7	40	20.2 ± 3.3B	51.2 (47.7–54.3)	59.2 (55.4–71.7)	2.9	3.5 (3.1–4.0)
	FS-S19	40	10.9 ± 1.2A	50.9 (45.7–55.0)	66.8 (61.2–78.3)	27.9[b]	4.0 (3.5–4.5)
Worker	FW-S9	40	8.4 ± 1.3A	11.8 (10.9–12.6)	16.8 (15.5–19.0)	0.0	1.0
	FW-U8	40	10.7 ± 1.2A	22.7 (20.2–25.0)	30.0 (27.0–36.5)	7.1[b]	1.8 (1.6–2.0)
	FW-S7	40	28.1 ± 4.2B	35.9 (34.9–36.8)	39.8 (38.5–42)	0.6	2.4 (2.1–2.7)
	FW-S19	40	12.9 ± 2.2A	22.1 (21.0–23.4)	27.8 (25.7–31.9)	0.7	1.7 (1.4–1.9)
Permethrin (5.26)							
Soldier	FS-S9	40	7.5 ± 0.7AC	47.4 (44.9–49.6)	70.2 (66.1–76.2)	2.2	1.9 (1.6–2.3)
	FS-U8	40	8.2 ± 0.8ABC	96.5 (90.3–102.2)	138.1 (126.5–160.0)	16.8[b]	3.7 (3.1–4.4)
	FS-S7	40	10.3 ± 1.1BC	94.3 (75.1–104.5)	125.6 (111.8–187.7)	92.8[b]	3.4 (2.9–4.0)
Worker	FW-S9	40	6.5 ± 1.0A	23.6 (16.5–27.4)	37.1 (31.2–68.1)	5.1	1.0
	FW-U8	40	2.8 ± 0.4E	38.7 (26.2–47.4)	110.8 (93.9–148.5)	27.7[b]	3.0 (2.2–4.0)
	FW-S7	40	9.6 ± 1.1BC	44.9 (42.2–47.0)	60.9 (57.9–65.3)	6.6	1.6 (1.4–2.0)
	FW-S19	40	4.0 ± 0.3D	83.5 (78.7–89.3)	176.2 (153.9–211.7)	7.9	4.8 (3.7–6.1)
Cypermethrin (5.26)							
Soldier	FS-S9	40	10.2 ± 1.3A	20.8 (19.6–22.0)	27.9 (26.0–31.)	1.1	1.3 (0.9–1.7)
	FS-U8	40	5.3 ± 0.6B	28.5 (21.6–33.0)	49.6 (43.4–62.5)	19.8[b]	2.2 (1.7–3.0)
	FS-S7	40	9.7 ± 1.1AC	46.7 (37.3–54.8)	63.2 (54.1–110.7)	40.9[b]	2.9 (2.1–3.9)
	FS-S19	40	4.6 ± 0.7BCD	108.2 (101.1–119.2)	204.8 (169.7–287.5)	3.0	9.2 (6.4–13.3)
Worker	FW-S9	40	4.7 ± 0.8BCDE	11.4 (10.0–13.2)	21.3 (17.2–31.7)	0.1	1.0
	FW-U8	40	8.1 ± 0.7AC	18.8 (17.5–20.1)	26.5 (24.5–30.0)	0.6	1.2 (0.9–1.6)
	FW-S7	40	8.1 ± 0.7ACF	34.1 (31.6–36.4)	49.2 (45.4–54.8)	12.8[b]	2.2 (1.6–3.0)
	FW-S19	40	6.5 ± 0.6DEF	48.4 (45.1–51.6)	76.5 (69.8–87.5)	13.5[b]	3.4 (2.6–4.6)
Deltamethrin (0.053)							
Soldier	FS-S9	40	10.9 ± 1.4A	31.8 (22.7–35.9)	41.7 (37.0–57.0)	31.3[b]	1.5 (1.4–1.6)
	FS-U8	40	7.6 ± 0.8B	61.4 (58.8–64.2)	90.3 (83.2–101.8)	5.5	2.2 (2.0–2.2)
	FS-S19	40	5.5 ± 0.6C	191.2 (181.2–200.5)	328.1 (298.9–369.3)	7.0	11.6 (10.3–13.2)
Worker	FW-S9	40	13.6 ± 1.3ABD	21.0 (19.8–22.5)	27.9 (25.5–32.8)	0.4	1.0
	FW-U8	40	10.1 ± 1.2ABD	37.5 (34.7–39.8)	50.2 (46.4–57.4)	4.0	1.8 (1.6–2.1)
	FW-S7	40	2.9 ± 0.4E	165.8 (150.2–191.8)	456.6 (346.7–708.5)	5.0	16.0 (11.9–21.5)
	FW-S19	40	6.1 ± 0.9BC	250.0 (227.7–294.7)	404.2 (331.7–578.4)	8.7[b]	14.2 (10.7–18.8)
Bendiocarb (2.63)							
Soldier	FS-S9	40	13.7 ± 2.1A	68.1 (65.0–70.7)	84.5 (80.4–91.7)	0.5	3.3 (2.9–3.7)
	FS-U8	40	9.0 ± 0.8A	51.8 (45.2–56.6)	71.9 (65.2–85.9)	38.0[b]	2.9 (2.5–3.2)
	FS-S7	40	6.5 ± 0.8B	30.3 (25.8–34.4)	47.8 (40.7–68.4)	9.5[b]	1.9 (1.6–2.2)
	FS-19	40	15.1 ± 2.5A	39.7 (37.8–41.3)	48.2 (45.8–52.8)	1.4	3.3 (2.9–3.7)
Worker	FW-S9	40	8.9 ± 1.1A	23.2 (19.6–26.7)	32.4 (27.8–47.8)	6.0	1.3 (1.1–1.5)
	FW-U8	40	13.9 ± 2.6A	46.7 (43.7–48.6)	57.7 (55.0–63.0)	0.7	2.3 (2.1–2.6)
	FW-S7	40	9.6 ± 1.0A	34.8 (32.1–37.6)	47.4 (49.9–56.2)	8.3[b]	1.9 (1.6–2.1)
	FW-S19	40	11.5 ± 1.7A	19.8 (18.7–20.9)	25.6 (23.7–29.0)	0.7	1.0
Fipronil (630.65)							
Soldier	FS-U8	40	48.7 ± 6.6C	366.3 (362.6–369.7)	389.1 (383.6–398.0)	0.4	1.5 (1.4–1.6)
Worker	FW-S9	40	7.4 ± 0.7A	164.2 (157.2–171.7)	249.4 (227.8–271.8)	2.9	1.0 (0.9–1.2)
	FW-U8	40	19.0 ± 4.8B	219.7 (211.5–225.2)	256.7 (244.4–295.0)	1.9	1.1 (1.0–1.1)
	FW-S7	40	12.4 ± 0.8B	189.3 (185.9–193.1)	240.1 (234.3–247.5)	4.8	1.0
	FW-S19	40	10.4 ± 0.6B	248.7 (243.0–255.2)	330.2 (315.5–349.3)	19.0[b]	1.4 (1.3–1.5)
Fipronil (630.65+526.13 oil)							
Soldier	FS-U8	40	16.8 ± 2.2A	229.7 (222.8–236.1)	273.9 (263–291.2)	0.2	1.1 (1.0–1.2)
Worker	FW-S9	40	9.7 ± 0.8B	182.7 (177.3–188.1)	247.9 (236.2–264.1)	5.7	1.0
	FW-U8	40	18.1 ± 2.1A	225.9 (219.7–230.8)	265.9 (258.5–277.0)	4.0	1.2 (1.1–1.4)
	FW-S7	40	10.9 ± 0.8BA	230.4 (226.1–235.2)	302.3 (290.1–318.7)	16.8[b]	1.2 (1.1–1.4)
	FW-S19	40	6.6 ± 0.6C	300.0 (284.8–321.2)	469.0 (420.3–545.5)	16.0[b]	1.9 (1.5–2.3)

[a] Slopes followed by the same letter indicate the hypothesis that the lines are parallel cannot be rejected when P is > 0.05.
[b] Chi-square exceeds tabular $P = 0.05$ value.

Table 2. Insecticide Susceptibility in *Coptotermes formosanus* soldiers from different colonies

Insecticide ($\mu g/cm^2$) ratio	Colony	Susceptibility LT_{90} (95% CI)[a]
Chlordane (630.65)		
	FS-S9	1.0
	FS-U8	2.0 (2.0–2.1)
	FS-S7	1.1 (1.0–1.2)
	FS-S19	1.1 (1.1–1.2)
Methoxychlor (5260.00)		
	FS-S9	1.0
	FS-U8	1.8 (1.6–2.0)
Chlorpyrifos (626.13)		
	FS-S9	1.0
	FS-U8	1.1 (0.2–4.8)
	FS-S7	1.5 (0.3–6.7)
	FS-S19	1.7 (0.4–7.6)
Permethrin (5.26)		
	FS-S9	1.0
	FS-U8	1.1 (1.0–1.2)
	FS-S7	3.4 (2.9–4.0)
Cypermethrin (5.26)		
	FS-S9	1.0
	FS-U8	1.8 (1.7–2.0)
	FS-S7	2.3 (2.0–2.6)
	FS-S19	7.4 (5.8–9.4)
Deltamethrin (0.053)		
	FS-S9	1.0
	FS-U8	2.2 (2.0–2.4)
	FS-S19	7.8 (7.0–8.6)

[a] Susceptibility ratio and confidence interval (±95% CI) calculated by the method of Robertson and Preisler (1992).

in the 8-h bioassay. Soldiers from colony U8 were 1.8 times less susceptible than soldiers from S9 (Table 2). Soldiers from U8, collected from a former military facility and one of the sites of first introduction of *C. formosanus,* had an unusual dose-mortality curve with several step like plateaus in the region above 60% mortality (Fig. 3). The unusual curve of U8 soldiers was reflected in its high chi-square value (Table 1). Workers and soldiers from the other colonies did not show notable differences in their tolerance ratio to methoxychlor (1.5 times maximum). There were two colonies in which soldiers were more susceptible than workers at the LT_{50} level and one colony at the LT_{90} level.

Chlorpyrifos resulted in a maximum LT_{90} tolerance ratio in *C. formosanus* workers of 2.4 X. S9 and S7 were the most and lest susceptible, respectively (Table 1). The dose-mortality curves show the significant differences between colonies (Table 1; Fig. 1). S9 was located furthest from visible structures and had minimal pressure from lawn care and pest control chemicals. Again, theoretically, this colony was subjected to less insecticide pressure. Soldiers were significantly less susceptible than their respective workers for all colonies. The most susceptible soldiers and workers came from the same colony, S9 (Table 1). These results contrast with the Gatti and Henderson's (1996) study, which found that soldiers were more susceptible to chlorpyrifos than workers. This contrast may reflect variation between colonies or differences in experimental design. S19 soldiers displayed a substantial plateau above ≈90% mortality in the dose–response

curve to chlorpyrifos (Fig. 1). Soldiers from colony S19 were 1.7 times less susceptible to chlorpyrifos than soldiers from colony S9 (Table 2).

For permethrin, LT_{90} tolerance ratios for *C. formosanus* workers included 4.8 times for colony S19 and 3.0 times for colony U8. Again, workers of colony S9 were most susceptible. Workers from U8 had ≈20% of the test insects plateau to almost flat in their dose-mortality curve (Fig. 1). The dose-mortality curve for U8 soldiers also plateaus to nearly flat at ≈80% mortality (Fig. 1). Soldiers from colony S19 (the proposed young colony) did not die when exposed to the diagnostic dose of permethrin. Thus, permethrin treatments had two colonies at the LT_{90} and four colonies at the LT_{50} level in which the soldiers were significantly less susceptible than the workers from their respective colonies. Soldiers from U8 and S7 were 3.7 and 3.4 times less susceptible than workers from the most susceptible colony (S9). With permethrin, the most susceptible workers and soldiers were from the same colony (S9). The highest intra-soldier tolerance ratio was between S9 and S19 (7.4 X; Table 2).

Coptotermes formosanus workers displayed cypermethrin tolerance ratios of 3.4 and 2.2 times in colonies S19 and S7, respectively (Table 2). As with permethrin, S9 was most susceptible. Dose mortality slope flattening was evident in S7 and S19 workers (Fig. 2). Cypermethrin treatments had two and four colonies in which soldiers had significantly higher susceptibility than workers at the LT_{90} and LT_{50} levels, respectively. S19 soldiers were 9.2 times less susceptible than the most susceptible workers from S9 (Table 1) and 7.4 times less susceptible than the most susceptible soldiers from S9 (Table 2). With cypermethrin, the most susceptible workers and soldiers came from the same colony, S9. Slope flattening was evident in the dose mortality plots of U8 and S7 soldiers (Fig. 2). Only partial mortality was achieved in S19 soldiers (Fig. 2).

Deltamethrin exposed *C. formosanus* workers from colonies S7 and S19 had tolerance ratios of 16.0 and 14.2 X, respectively (Table 1). Dose-mortality slopes for workers from S7 and S19 were significantly flatter than for the other colonies tested and only partial mortality was achieved (Fig. 2). Soldiers from S19 were 11.6 times less susceptible than the most susceptible workers from S9 (Table 1) and 7.8 times less susceptible than the most susceptible soldiers from S9 (Table 2). With deltamethrin, the most susceptible workers and soldiers came from S9. Soldiers from S7 were not killed by deltamethrin after 8 h. In two of the colonies (S9 and U8) the soldier's lethal time to mortality values were significantly greater than their respective workers. In one colony, the soldiers were numerically but not significantly less susceptible than workers from the same colony. Gatti and Henderson (1996) found no difference in susceptibility between soldiers and workers after pooling the data from five tested colonies of *C. formosanus,* in which colony differences could not be detected. S19 soldier's dose-mortality curve was significantly flatter when compared with soldiers from U8 that was significantly
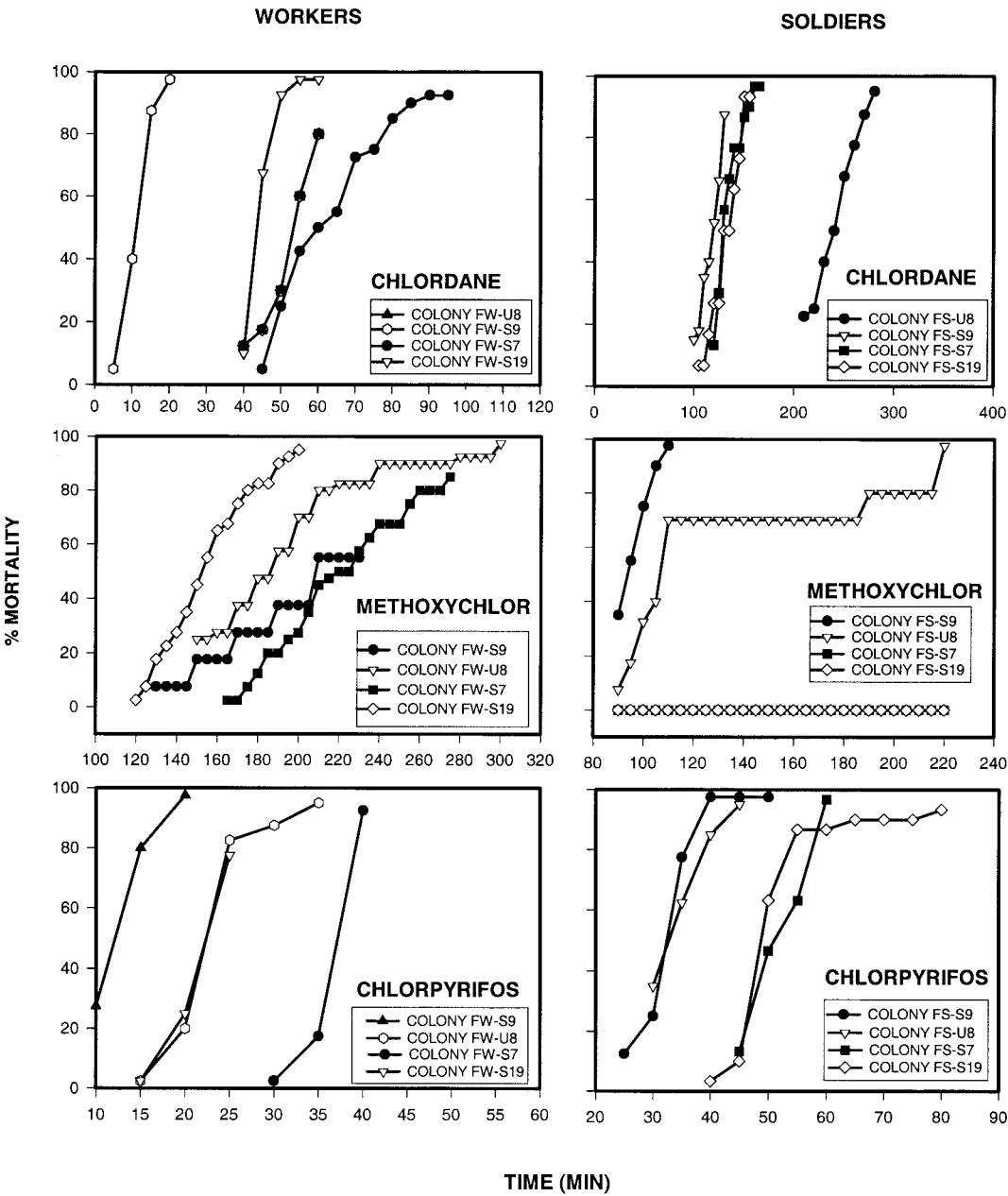
C. formosanus

Fig. 1. Lethal time to mortality plots of *C. formosanus* workers and soldiers exposed to chlordane (630.65 $\mu g/cm^2$), methoxychlor (5.261 mg/cm^2), and chlorpyrifos (526.13 $\mu g/cm^2$).

flatter than S9 (Table 1; Fig. 2). Soldiers from colony S19 were significantly less susceptible of deltamethrin than soldiers from colony U8, which were significantly less susceptible than soldiers from colony S9 (Tables 1 and 2).

Bendiocarb exposed *C. formosanus* workers from colony U8 were 2.3 times less susceptible than the most susceptible workers from S19 (Table 1; Fig. 2).

While S19 had relatively low susceptibility to the pyrethroids tested, it was sensitive to carbamate. Worker dose-mortality curves had similar slopes. Soldiers from U8 displayed a substantial plateau in the dose-mortality curve (Fig. 2). Bendiocarb treated soldiers were significantly less susceptible than workers in two and three colonies at the LT_{50} and LT_{90} levels, respectively (Table 1).
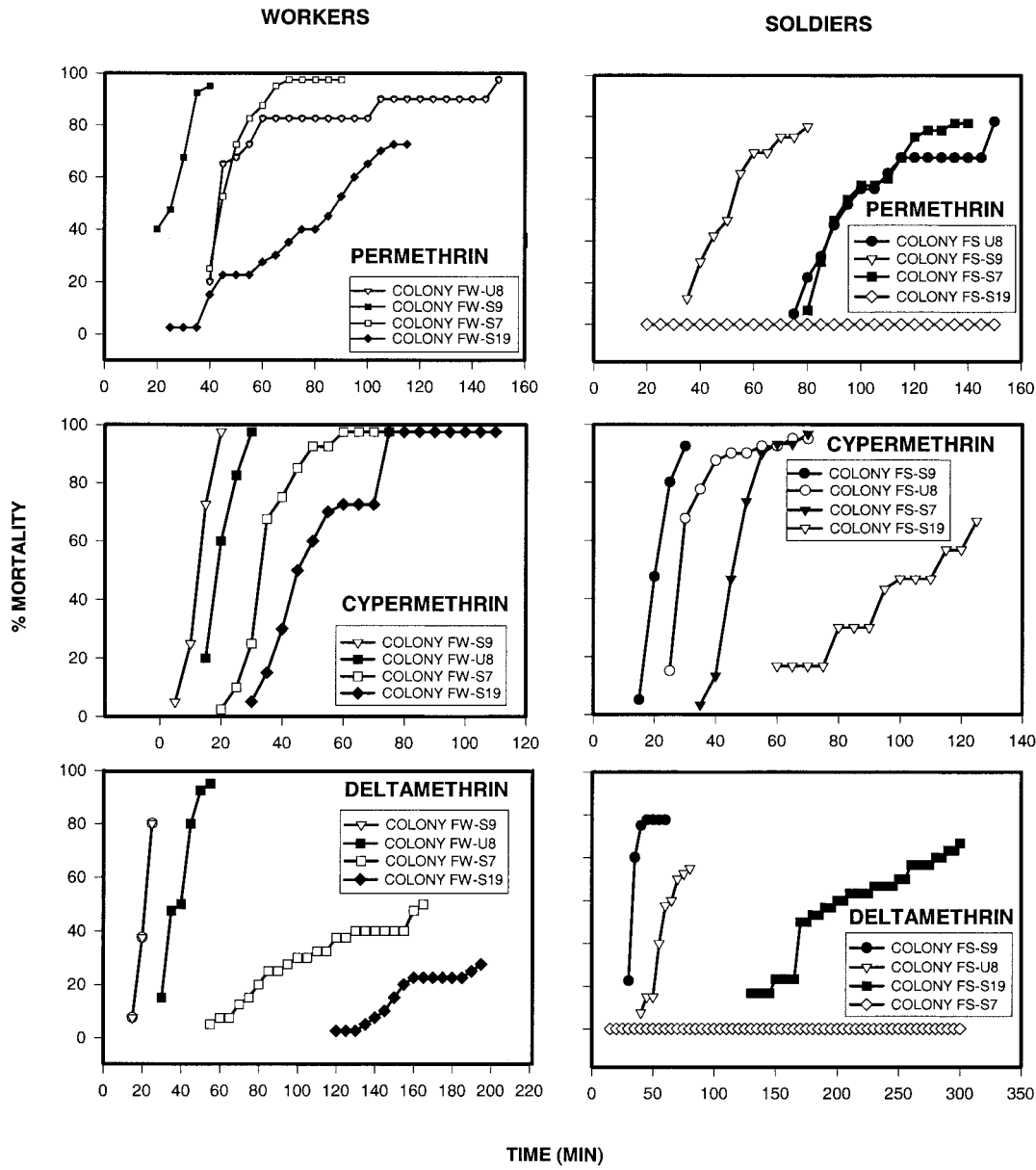
C. formosanus

Fig. 2. Lethal time to mortality plots of *C. formosanus* workers and soldiers exposed to permethrin (5.261 $\mu g/cm^2$), cypermethrin (5.261 $\mu g/cm^2$), and deltamethrin (0.053 $\mu g/cm^2$).

Fipronil did not kill *C. formosanus* soldiers from S9, S7, or S19 in the 8-h bioassay. Soldiers from U8 and workers from all colonies had similar tolerance ratios (Table 2). Soldiers from U8, the only colony killed, had a steep dose-response slope of 48.7 (Table 1; Fig. 3). Workers from U8, S7, and S19 had slopes not significantly different from each other. Fipronil with oil also failed to kill *C. formosanus* soldiers from S9, S7, or S19. The soldiers from U8 and workers from all

colonies had similar tolerance ratio (Table 1). The presence of oil flattened the slope of U8 when compared with the treatment without oil.

Reticulitermes virginicus. LT_{50}s, LT_{90}s, and slopes for workers are reported in Table 3. There was no mortality in the solvent controls. Results of tests with chlordane indicated that the slopes of colonies C21 and C26 were significantly flatter than the slopes of C71 and C2. Additionally, colony C2 was significantly
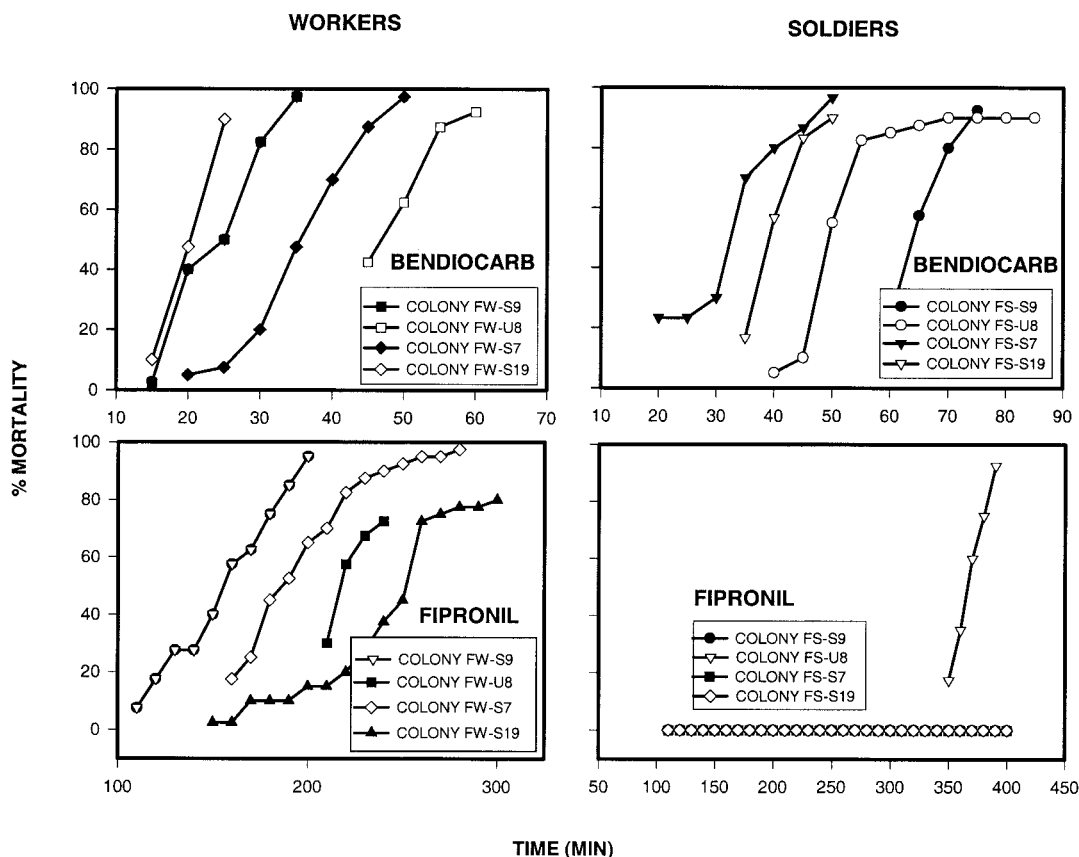
C. formosanus

Fig. 3. Lethal time to mortality plots of *C. formosanus* workers and soldiers exposed to bendiocarb (2.63 $\mu g/cm^2$) and fipronil (630.65 $\mu g/cm^2$).

more susceptible to chlordane than the other three colonies. Colony C2 also was the only colony that did not exhibit a flattening of its slope in the final ≈20% mortality (Fig. 4). The sequential order of colony susceptibility in this study was identical to the sequence of in vitro epoxidase activity levels isolated from the same colonies in which the conversion of aldrin to dieldrin was the model substrate (Valles et al. 1998). Similar detoxification mechanisms of the two cyclodienes are suspected and demonstrate a relationship between termite biochemical activity and the bioassay. Some flattening of the LT curve was observed with C26 (Fig. 4). Comparison of the pooled LT_{90}s of *C. formosanus* with *R. virginicus* showed no significant difference between spp. with chlordane (Table 4).

There were no significant differences in slopes among *R. virginicus* colonies treated with methoxychlor (Table 3). There were, however, significant differences in tolerance ratios. C71 was nearly three times less susceptible to methoxychlor than C21, the most susceptible colony (Table 3; Fig. 4). *Coptotermes formosanus* had significantly larger pooled worker

mean LT_{90} values (≈2X) than *R. virginicus* ($t = 3.21$, df = 6, $P = 0.0183$; Table 4).

Three *R. virginicus* colonies exposed to chlorpyrifos (C21, C26, and C71) had significantly flatter slopes than C2 (Table 3). C21 was the least susceptible colony to chlorpyrifos, with a nearly 3 times tolerance ratio compared with C2. C2, in addition to being the most susceptible colony, also had the steepest slope. This result is consistent with what would be expected from a susceptible homogenous population (Matsumura 1985). Colonies C21 and C26 possessed substantial flattening of the time-mortality slope's final ≈20% of the surviving termites (Table 3; Fig. 4). There was no significant difference between the pooled LT_{90}s of *C. formosanus* workers compared with *R. virginicus* workers exposed to chlorpyrifos (Table 4).

Permethrin intoxication of *R. virginicus* caused significantly flatter slopes in C26 and C2 than C21 and C71 (Table 3; Fig. 4). Colony C2, with the flattest slope, also possessed the fastest LT_{90}. This is unexpected, and probably reflects the large differences between colonies (Matsumura 1985), such that a population with a high degree of heterogeneity may still

Table 3. Insecticide susceptibility in *Reticulitermes virginicus* colonies

Insecticide ($\mu g/cm^2$)	Colony	N	Slope $\pm$ SE[a]	LT_{50} (95% FL) (min)	LT_{90} (95% FL) (min)	χ^2	Susceptibility ratio LT_{90} (95% CI)
Chlordane (630.65)	C21	40	6.6 ± 0.6A	26.6 (23.4–29.6)	41.5 (36.4–51.3)	16.1[b]	1.3 (1.1–1.4)
	C26	40	6.4 ± 0.8A	34.4 (27.2–38.9)	54.3 (48.1–68.3)	18.2[b]	1.7 (1.5–1.9)
	C71	40	11.2 ± 1.0B	37.8 (32.7–42.9)	49.2 (43.2–67.4)	33.3[b]	1.5 (1.4–1.7)
	C2	40	13.1 ± 1.7B	26.1 (24.9–27.3)	32.7 (30.9–35.5)	0.8	1.0
Methoxychlor (5.261)	C21	40	6.8 ± 0.8A	47.5 (44.8–49.9)	73.2 (67.2–83.2)	3.5	1.0
	C26	40	7.1 ± 0.5A	88.8 (85.3–91.6)	133.9 (125.7–145.1)	3.2	1.8 (1.6–2.1)
	C71	40	5.3 ± 0.7A	119.9 (112.4–131.6)	208.6 (177.7–270.6)	1.7	2.9 (2.2–3.6)
	C2	40	6.8 ± 0.7A	72.9 (70.0–76.1)	112.5 (103.9–125.7)	2.3	1.5 (1.3–1.8)
Chlorpyrifos (526.13)	C21	40	3.1 ± 0.3A	25.1 (20.8–28.7)	64.9 (56.3–79.1)	17.7[b]	2.8 (2.6–3.2)
	C26	40	3.0 ± 0.4A	16.2 (12.5–19.1)	43.8 (37.4–55.4)	2.4	1.9 (1.6–2.3)
	C71	40	7.7 ± 1.0B	18.8 (17.2–20.1)	27.5 (25.4–30.9)	1.3	1.2 (1.1–1.3)
	C2	40	11.0 ± 1.7B	17.5 (16.4–18.5)	22.9 (21.3–25.7)	0.1	1.0
Permethrin (5.261)	C21	40	11.2 ± 1.1A	33.7 (31.2–36.3)	47.1 (43.3–52.3)	7.7	1.4 (1.2–1.6)
	C26	40	7.9 ± 0.8B	30.6 (28.3–33.0)	42.9 (39.5–47.3)	2.1	1.4 (1.2–1.6)
	C71	40	15.2 ± 2.5A	27.3 (24.6–30.1)	38.2 (34.4–43.1)	3.6	1.0 (0.9–1.2)
	C2	40	6.8 ± 0.9B	21.4 (19.5–23.3)	29.9 (27.3–33.4)	5.4	1.0
Cypermethrin (5.261)	C21	40	8.7 ± 1.3A	25.7 (23.8–27.7)	32.8 (30.2–36.7)	0.4	1.8 (1.6–2.1)
	C26	40	14.3 ± 2.1B	20.0 (18.2–21.9)	25.5 (23.2–29.0)	0.4	1.2 (1.1–1.4)
	C71	40	14.6 ± 2.8B	16.1 (14.8–17.4)	20.5 (18.9–23.0)	4.0	1.0
	C2	40	15.8 ± 2.3B	19.5 (17.8–21.4)	24.9 (22.6–28.3)	1.3	1.2 (1.1–1.3)
Deltamethrin (0.053)	C21	40	13.5 ± 1.4A	55.8 (53.1–58.5)	75.9 (71.9–80.5)	2.2	1.0 (0.9–1.1)
	C26	40	7.9 ± 0.6B	54.0 (51.7–56.2)	73.4 (70.0–77.4)	4.3	1.1 (1.0–1.2)
	C71	40	9.3 ± 0.9B	51.0 (48.7–53.4)	69.4 (66.0–73.6)	6.2	1.0
	C2	40	13.6 ± 1.3A	56.9 (54.3–59.8)	77.5 (73.1–82.8)	13.1[b]	1.0 (0.9–1.1)
Bendiocarb (2.63)	C21	40	16.1 ± 2.5C	28.4 (25.5–31.3)	38.7 (34.9–44.1)	2.4	1.7 (1.5–2.0)
	C26	40	6.8 ± 0.9A	13.4 (12.0–14.9)	18.3 (16.4–21.0)	0.1	1.0
	C71	40	10.8 ± 1.1B	43.7 (40.7–46.8)	59.6 (54.9–66.8)	3.7	2.9 (2.5–3.3)
	C2	40	9.8 ± 1.7AB	17.2 (15.4–19.3)	23.5 (20.8–27.5)	1.7	1.2 (1.0–1.4)
Fipronil (630.65)	C21	40	10.5 ± 0.9B	283.0 (274.5–291.9)	400.1 (383.7–419.4)	4.7	1.2 (1.1–1.4)
	C26	40	7.5 ± 0.7A	250.5 (243.0–258.1)	354.1 (341.0–369.3)	7.4	1.2 (1.1–1.4)
	C71	40	9.2 ± 0.8AB	219.6 (212.2–227.0)	310.5 (299.1–323.4)	1.9	1.0
	C2	40	7.9 ± 0.6A	332.5 (323.3–342.3)	470.0 (450.6–493.1)	7.0	1.6 (1.5–1.8)
Fipronil (630.65+526.13 Oil)	C21	40	4.9 ± 0.9B	49.0 (35.6–63.8)	110.0 (81.9–187.0)	0.2	1.7 (1.4–2.1)
	C26	40	6.0 ± 0.9B	49.6 (36.0–64.7)	111.1 (82.6–190.1)	2.8	1.6 (1.3–1.9)
	C71	40	1.8 ± 0.5A	48.3 (34.0–60.7)	108.5 (85.0–163.7)	1.8	3.1 (1.6–6.0)
	C2	40	6.7 ± 1.3B	30.5 (20.3–40.2)	68.5 (51.7–106.3)	7.3	1.0

[a] Slopes followed by the same letter indicate the hypothesis that the lines are parallel cannot be rejected when *P* is > 0.05.

be less tolerant than a population with a lower degree of heterogeneity. There was no significant difference in susceptibility to permethrin between the pooled LT_{90}s of *C. formosanus* when compared with *R. virginicus* (Table 4). However, two colonies of *C. formosanus* workers had significantly higher LT values than *R. virginicus.*

Cypermethrin treated *R. virginicus* showed a significantly flatter slope only with colony C21 (Table 3; Fig. 4). Colony C21 was significantly the least susceptible to cypermethrin (1.8X). There was no significant difference between the pooled LT_{90}s of *C. formosanus* compared with *R. virginicus* (Table 4). However, workers from two *C. formosanus* colonies (S7 and S19) had significantly greater LT values than *R. virginicus* (Tables 1 and 3).

Deltamethrin treatment resulted in little difference among *R. virginicus* colony's tolerance ratios, but colonies C71 and C26 had significantly flatter slopes than the other two colonies, caused by plateaus in the LT curve (Table 3; Fig. 4). There was no significant difference between the pooled LT_{90}s of *R. virginicus* and those for *C. formosanus* due to the large SD of *C. formosanus* caused by their 16 times tolerance ratio (Table 4). Pooled LT_{90} values for *R. virginicus* were numerically, but not significantly, lower than *C. for-*

mosanus. Workers from two colonies of *C. formosanus* had significantly higher LT values (S7 and S10) than the least susceptible *R. virginicus* colony exposed to deltamethrin (Tables 1 and 3). However, two *C. formosanus* colonies also had significantly lower LT values (S9 and U8) than most susceptible *R. virginicus* colony.

Bendiocarb treated *R. virginicus* had a significant tolerance ratio of 2.9 times between the most and least susceptible *R. virginicus* colonies, C26 and C71, respectively (Table 3). As with permethrin, the most sensitive colony possessed the flattest slope (Fig. 5). There was no clear trend in susceptibility between *C. formosanus* and *R. virginicus* to bendiocarb (Tables 1 and 3).

In this study fipronil was comparatively slow acting as a contact poison. There were little inter-colony differences in the response of *R. virginicus* to fipronil (Fig. 5). *Reticulitermes virginicus* had a significantly higher pooled LT_{90} than *C. formosanus.* The addition of 1.0% oil substantially increased fipronil's speed of intoxication for all colonies of *R. virginicus* but not *C. formosanus.* The addition of oil to fipronil also increased the tolerance ratio of C71 from the most susceptible to the least susceptible (≈3X). Workers of
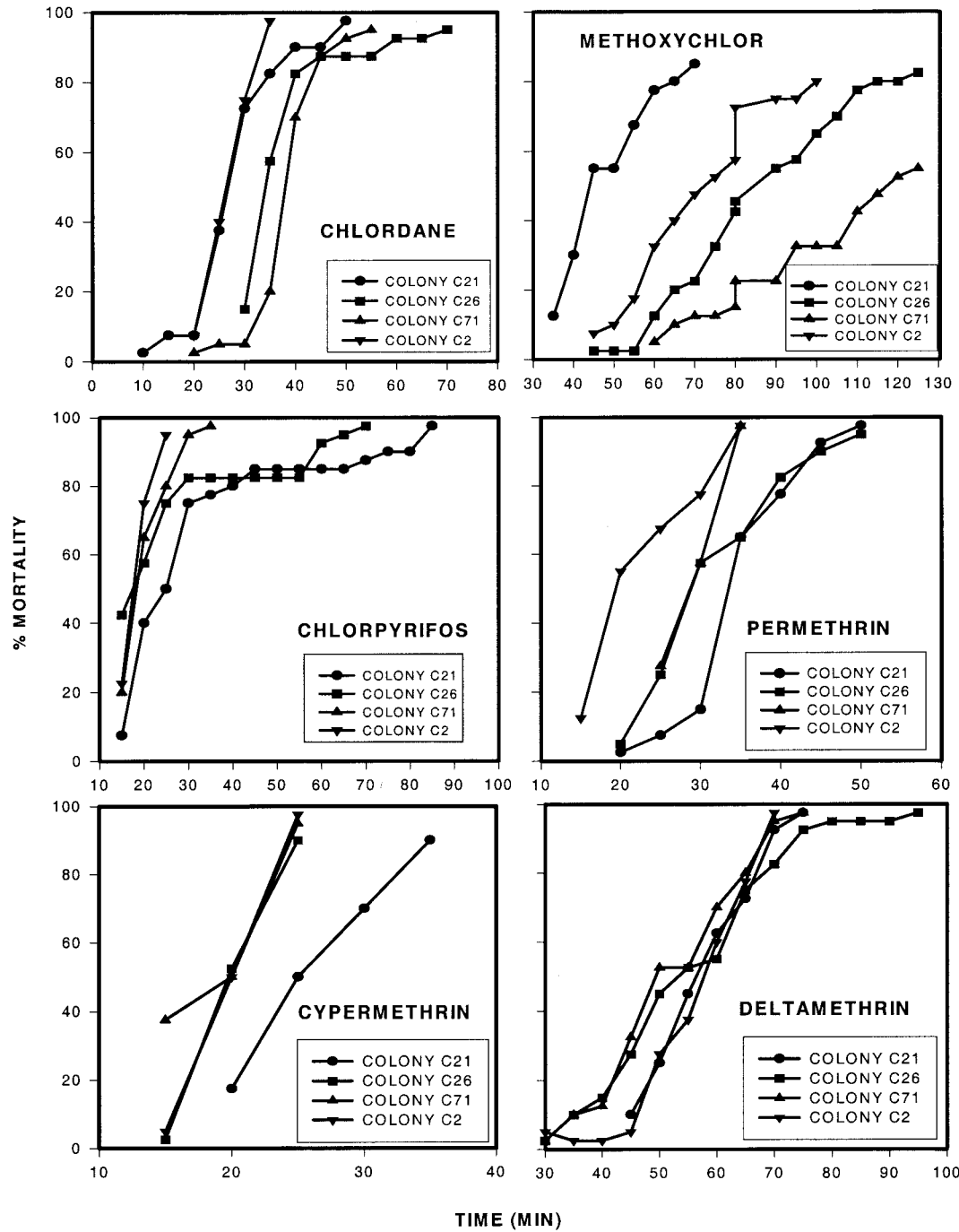
R. virginicus WORKERS

Fig. 4. Lethal time to mortality plots of *R. virginicus* workers exposed to chlordane (630.65 μg/cm^2), methoxychlor (5.261 mg/cm^2), chlorpyrifos (526.13 μg/cm^2), permethrin (5.261 μg/cm^2), cypermethrin (5.261 μg/cm^2), and deltamethrin (0.053 μg/cm^2).

Table 4. Comparison of pooled LT_{90} between *C. formosanus* and *R. virginicus* workers

Insecticide	*C. formosanus*	*R. virginicus*	P^a
	(mean ± SD)		
Chlordane	54.9 ± 29.3	44.4 ± 9.421.	0.5209
Methoxychlor	265.3 ± 60.3	132.1 ± 56.9	0.0183
Chlorpyrifos	28.6 ± 9.4	39.5 ± 7.4	0.1179
Permethrin	96.3 ± 61.5	39.5 ± 7.4	0.1168
Cypermethrin	43.4 ± 25.19	25.9 ± 5.1	0.2233
Deltamethrin	234.7 ± 227.1	74.1 ± 3.53	0.2069
Bendiocarb	40.8 ± 14.5	35.0 ± 18.5	0.6424
Fipronil	269.1 ± 41.3	383.7 ± 68.2	0.0283
Fipronil + Oil	321.3 ± 101.0	99.5 ± 20.7	0.0051

^{a} *t*-test.

R. virginicus were significantly more susceptible to fipronil + oil than *C. formosanus* (Tables 1, 3, and 4).

Coptotermes formosanus workers had significantly larger pooled LT_{90} values than *R. virginicus* with methoxychlor and fipronil + oil. *Coptotermes formosanus* had numerically larger LT_{90} values than *R. virginicus* with every insecticide except chlorpyrifos and fipronil. Fipronil provided a significantly larger pooled LT_{90} value for *R. virginicus*. The pooled LT_{90} for *C. formosanus* on deltamethrin was numerically >3× *R. virginicus*, but the SD of *C. formosanus* was nearly as large as the mean, reflecting differences in colony susceptibility. Beal and Smith (1971) found it took longer to kill *C. formosanus* in soil plate tests with chlordane than it did to kill either *R. virginicus* or *R. flavipes* (Kollar). Su and Scheffrahn (1990) found through topical applications that *C. formosanus* was consistently less susceptible to insecticides than *R. flavipes.* Osbrink et al. (1987) also found *C. formosanus* to be less susceptible to the fumigant sulfuryl fluoride

than the other rhinotermitids tested. Though mass was not determined for the specific *R. virginicus* colonies tested here, individual workers weighed ≤2.5 mg (unpublished data) which places them in the same size range as the two smaller colonies of *C. formosanus* (S19 and S7). There was no indication that smaller *C. formosanus* workers were more sensitive to insecticides using this contact bioassay.

Because of the changes in subterranean termite control technologies, e.g., baits and nonrepellent termiticides, termite-pesticide interactions require study. Notably there were large inter-colony differences in response to insecticides that support the suggestion of Su and La Fage (1984) to use multiple colonies when conducting bioassays. Also, there were instances where a part of a termite population within a colony responded differently to toxicants. A portion of the colony may have a different genotype, possibly mutant traits were present, or different phenotypic representation of the same genotype was expressed. The latter could reflect differences in insect age, time since last molt, or induction caused by feeding history (Matsumura 1985). Susceptibility differences raise questions regarding differential rates of insecticide penetration, metabolic resistance, and target-site insensitivity.

Considerable intra-colony variability occurred as indicated by the plateaus in the time-mortality curves. Some of the termites are less susceptible and may possess mechanisms that enhance detoxification or limit termiticide uptake. Intra-population slope differences with flattening of the last ≈20% of the LT plots reflect heterogeneous insect populations within the colony and may indicate transition to a state of insecticide resistance (Matsumura 1985). Development of less susceptible survivors of insecticide exposure into supplementary reproductive individuals the-
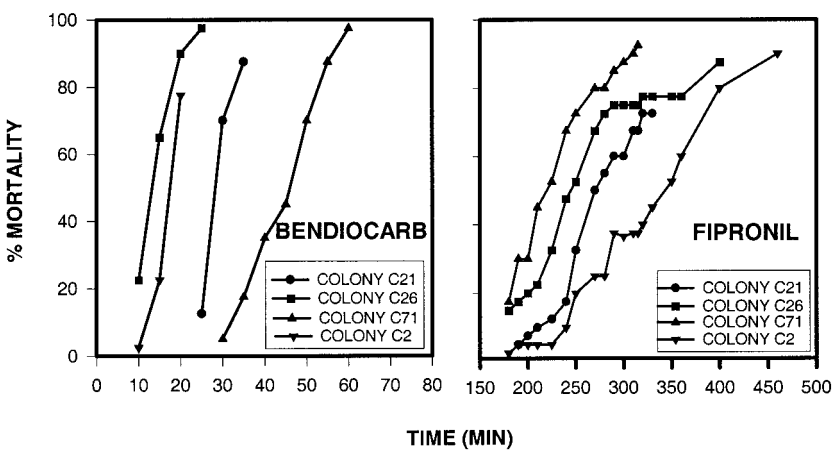
R. virginicus WORKERS

Fig. 5. Lethal time to mortality plots of *R. virginicus* workers exposed to bendiocarb (2.63 μg/cm^2) and fipronil (630.65 μg/cm^2).

oretically could lead to development of less susceptible colonies regardless of the mechanism. In nonsocial insects, a number of generations must be completed to substantially increase such gene frequency, making generation time critical to resistance development (Cochran 1995). With rhinotermitids, selection can take place at any stage that can develop into a supplementary or primary reproductive (imago). Supplementary reproductives can develop minimally from the first two instars and at least some brachypterous nymphs (Miller 1969, Lenz et al. 1988). Development of secondary reproductives from less susceptible individuals could increase gene frequency within a colony in a single generation due to their high reproductive rate. Because termite colonies are often a closed system, such traits could be very stable within the colony. The presence of susceptibility or resistance in an insect population often goes unnoticed until the frequency of the detoxification gene gets so high that control failures begin to occur (Cochran 1989). A theme in urban insect control indicates that small differences in susceptibility to insecticide allow for large changes in the ability of pests to circumvent control strategies (Rust and Reierson 1978). Failures to control subterranean termites are in the 20% range after the first year according to surveys of pest control operators in Kentucky and Ohio (Potter 2000). Failure rates are probably greater along the gulf coast due to greater subterranean termite pressure in this region (Kofoid 1934). It is generally believed that treatment failures are caused by incomplete termiticide coverage of the soil around or under the structure. Theoretically, treatment failures may also reflect decreased susceptibility in subterranean termite populations.

Acknowledgments

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